

LYONOTHAMNOXYLON FROM THE LOWER PLIOCENE OF WESTERN NEVADA

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At the northern end of Fish Lake Valley, Nevada, a desolate, arid valley between the White Mountains to the west and the Silver Peak Range to the east, there is a curiously eroded gully containing the remains of about seventy fossil trees (fig. 1). Although the trees are badly weathered and fragmented, it is possible to observe that all were preserved *in situ*, some in a standing position and others lying where they were felled by some agent such as a storm or flood.

Although the existence of the trees has been known for many years, no published descriptions have been found in the literature, nor, as far as I can determine, has there been any attempt to identify the wood. During a brief visit to the fossil locality in 1955 and a recent visit in 1964, fragments of wood were collected from each tree. The following account is based on a study of thin sections made from some of the fragments.¹

GEOLOGIC OCCURRENCE

The fossil locality is in Esmeralda County, T 1 N and R 35 E, three fourths of a mile south of hill 6061 on the Davis Mountain topographic sheet of the U.S. Geological Survey in the vicinity of the University of California Museum of Paleontology locality V-2804. The trees are embedded in a thick layer of sandstone several feet below the surface layer of white vitric tuff which in that particular area is one to two feet thick. Both sandstone and tuff appear to have been stream deposited. The beds dip to the southeast at an angle of forty to fifty degrees from the horizontal (fig. 1).

Several feet above the tree horizon and just below the layer of tuff the sandstone is green in color and contains mammalian bones. Stirton (1929; 1939) considered the fauna lower Pliocene in age and referable to the early Clarendonian using standard North American geochronology. Everndon et al (1964) using potassium-argon dating techniques found that biotite in the vitric tuff just below a micro-mammal layer in the vicinity of the fossil tree horizon gave a reading of 11.4 million years before Present. According to recent observations (Richard Tedford, personal communication) the dated biotite layer is, as far as can be determined, the same unit which occurs directly above the stump horizon and, therefore, also directly above Stirton's mammalian layer, thus corroborating his assignment of an early Pliocene age.

The fallen trees lie in a southeasterly direction. Some of the trunks are six or more ft. long, but no branches have been observed, nor is bark present. The upright stumps consist of the very base of the trunk and the basal root system. The surrounding matrix has been eroded away several

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ft below the original ground level, so that now some of the stumps rest on tall sandstone columns as much as 10 ft in circumference and over 15 ft high (fig. 2). Since all the trees lie at the same horizon in the sandstone, it can be assumed that they were contemporaries.

SYSTEMATIC DESCRIPTION

For the most part the wood collected is not well preserved. Many of the specimens are weathered and chalky with little or no cellular structure remaining. Even in those specimens which are reasonably well preserved the secondary walls of most of the cells are absent. It is possible, however, to determine that all the specimens are of the same kind of wood. Since samples were collected from at least seventy trees, it looks as though all the trees were of one kind.

In comparing thin sections of the fossil wood with sections of various modern woods it was found that the structural pattern of the fossil is similar to that of certain woody members of the Rosaceae. In detail of pattern the secondary wood of the monotypic genus *Lyonothamnus* appears to resemble the fossil most closely.

Lyonothamnoxylon nevadensis gen. et sp. nov. (figs. 3-6). Growth rings narrow, averaging less than 1 mm. in width; detectable with hand lens. Diffuse porous to semi-ring porous. Pores solitary, rounded or slightly angular averaging 27 by 44 μ ($14 \times 22 - 37 \times 55$) in diameter with longer axis in radial direction. Vessel elements 184-300 μ in length. Vessel walls were difficult to measure because of the absence of secondary walls in most cells, but on the basis of a few fragmentary walls it appears that they are about 8 μ thick. Intervascular pitting small and alternate. In two vessels it is possible to observe what are undoubtedly remnants of spiral thickening. Gum plugs present in nearly all vessels. Perforation plates simple, almost horizontal in large vessels to oblique in small vessels with "tails" evident in some elements. Axial parenchyma metatracheal-diffuse, 6-8 cells high; small pits on tangential and radial walls. Rays heterogeneous and homogeneous 2-4 cells wide (characteristically 2 cells wide). Heterogeneous rays with 2-4 marginal rows of square cells. Cells of some rays irregular in size; marginal cells tend to be larger than those of multi-seriate part. Height averages 427 μ (some almost 1 mm). Frequently two rays appear to be joined vertically. Uniseriate 1-20 (mostly 6-8) cells high, cells isodiametric in tangential view. Ray to vessel pitting small, alternate. Fibers or fiber tracheids make up bulk of ground tissue; average 430 μ in length. Bordered pits occur on both tangential and radial walls. A few cells are sufficiently well preserved to show that the walls are fairly thick.

Holotype: Nevada, Esmeralda Co., Fish Lake Valley, V. M. Page 5567, July 1955, Stanford Univ. Paleont. Type Coll. 8425.

DISCUSSION

Although the fossil compares well with the secondary wood of *Lyonothamnus* (figs. 7-10), there are a few differences. These differences are



FIG. 1. Northend of Fish Lake Valley. Just to right of center is a tall column topped by a fossil stump. Behind the stump and at the same horizon along a line 7 mm below surface layer is a series of knobs which represent exposed stumps.

not major and may reflect either environmental differences, position in the tree from which the specimens were derived, or genetic changes that have occurred in the genus during the time interval between the lower Pliocene and the present. The main differences can be found in the consistently broader rays of the extant species (mostly 3–4 cells wide), apparently more abundant axial parenchyma, and more pores per mm^2 with a tendency toward radial chains in spring wood. Considerable variation was observed in the samples of modern material available. Rays, for example, vary from predominantly two cells wide in slide 9329 from the Arnold Arboretum wood collection to eight cells wide in a small branch from a tree growing on the Stanford campus. Some samples are distinctly ring porous, whereas in others there is little difference in pore size between early and late wood (figs. 7, 8). The amount of parenchyma also varies from one sample to another. Similar variations can be observed among the many fossil specimens collected, although for the most part the over-all structural pattern is quite uniform. Such uniformity is to be expected, since all the fossil trees presumably were subjected to the same environmental conditions, whereas the trees from which the reference samples were taken were growing in a variety of habitats. Although the degree of variation was greater among the modern samples, such varia-

tion as has been observed is of the same kind in both the fossil and the extant species.

No evidence of spiral thickening was found in the fibers of the fossil, nor were septae observed. Spiral thickening occurs in most fibers and septae in a few in the extant species of *Lyonothamnus*. Their absence in the fossil is to be expected because of the absence of the secondary wall in the majority of cells. Macerations of the secondary wood of *L. floribundus* A. Gray ssp. *asplenifolius* (Greene) Raven and another member of the Rosaceae, *Heteromeles arbutifolia* (Lindl.) M. Roem., show that there is a series of transitional forms between tracheids and vessel elements on the one hand and tracheids and fibers on the other. These transitional forms are difficult to recognize in sections, particularly in the fossils, but because the elongated xylary elements in the fossil bear evidence of conspicuously bordered pits, it is assumed that similar transitional forms are present; that is, some of the pitted structures may be fiber tracheids, some may be fibers, and others may be narrow vessel elements.

There are several genera in the Rosaceae whose wood bears a general resemblance to that of the fossil. Most of these, however, can be eliminated from consideration after examining the composition of the Pliocene vegetation of the western Great Basin where only a few genera of the Rosaceae are represented in the fossil record, and these, with the exception of *Lyonothamnus* have their modern equivalents in non-arborescent forms. It has been shown that by Pliocene time the floral elements now represented in eastern United States and eastern Asia and also those now in northern areas, which constituted a substantial part of the early Miocene floras, were largely eliminated from southwestern United States. Equivalents of most of the species present in the western Great Basin in early Pliocene time can still be found in southwestern United States, although their ranges have been somewhat restricted. It would follow, therefore, that woody plants now occurring in that area might be expected to appear in late Tertiary deposits of the same general region. In addition to *Lyonothamnus*, *Heteromeles arbutifolia* is the only arborescent member of the Rosaceae found in southwestern United States whose wood bears a resemblance to the fossil. Thus far *Heteromeles* has not been found in any of the Pliocene or Mio-Pliocene deposits in the western Great Basin, whereas *Lyonothamnus* has appeared in three localities. All three of these localities (Aldrich Station, Middlegate, and Stewart Springs) are Mio-Pliocene in age, thus slightly older than the fossil wood locality, and in all three the genus is represented by leaf impressions. Leaf fragments ascribed to *Lyonothamnus* from the Aldrich Station and Middlegate floras (Axelrod, 1956) were subsequently thought to be *Comptonia*. They have now been returned to *Lyonothamnus* (Wolfe, in press).

Some differences between the wood of *Heteromeles* and the fossil indicate that close relationship between them is questionable. Vessel elements



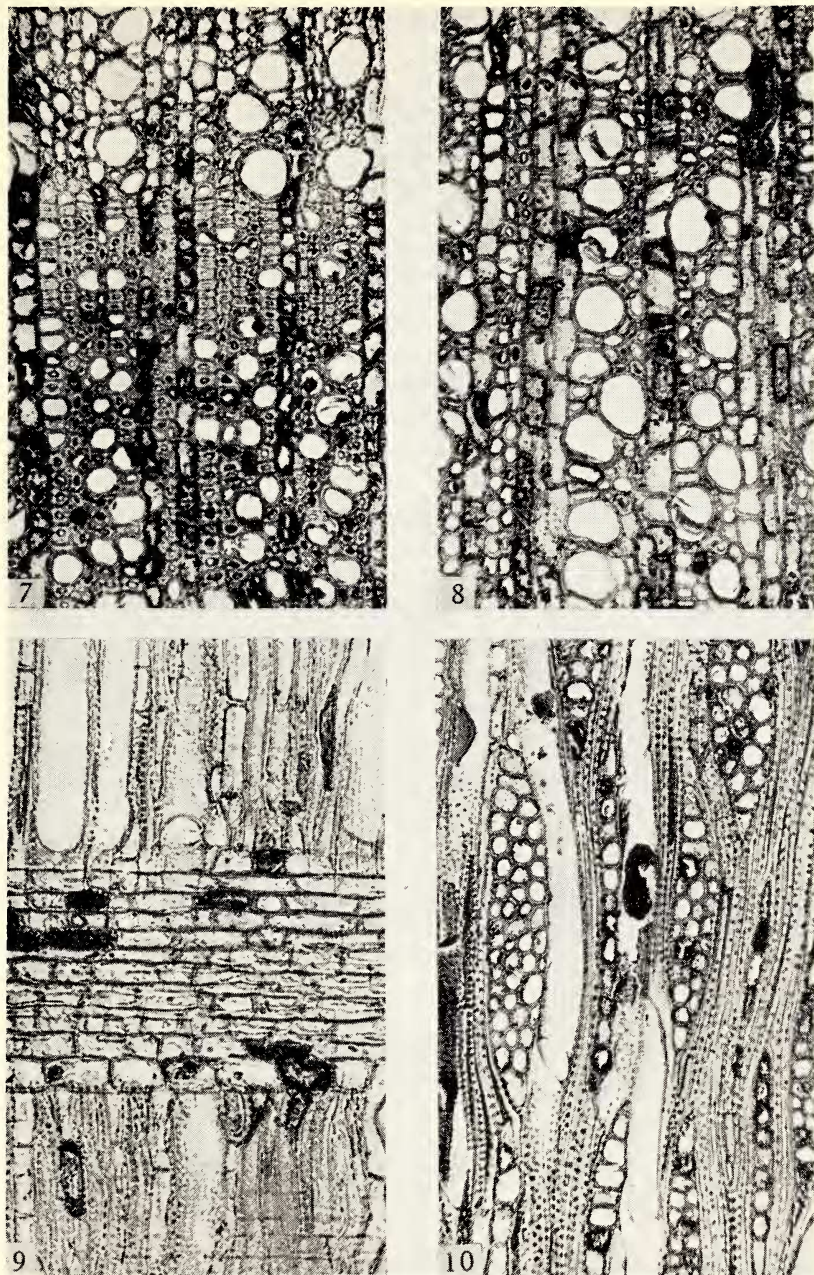
FIG. 2. Group of stumps resting on sandstone columns. Note that stump to the left appears to have two trunks.

in the secondary wood of *Heteromeles* average $600\ \mu$ in length, whereas those of the fossil average $270\ \mu$. The latter figure is more consistent with the $312\ \mu$ average in *Lyonothamnus*. Fibers in *Heteromeles* tend to be longer ($825\ \mu$ as opposed to an average of $430\ \mu$ in the fossil and in *Lyonothamnus*), and the uniseriate rays tend to be shorter (3–8 cells high as opposed to 1–18 cells high in the fossil and in *Lyonothamnus*). Comparisons were made of samples of *Heteromeles* collected from plants on the Stanford campus, a root and stem from Panoche Pass, California and samples from three trees of *L. floribundus* ssp. *asplenifolius* growing on the Stanford campus. Although vessel length is of doubtful value in wood identification, it is felt that, because the feature is consistent among the several specimens sampled of each species, the difference is real and can, therefore, be used together with the disparity in fiber length and ray height to point out the difference between the wood of *Heteromeles* and the fossil while at the same time emphasizing the similarity between the wood of *Lyonothamnus* and the fossil.

Growth habit provides another link between the fossil trees and *Lyonothamnus*. As described by Millspaugh and Nuttall (1923), *L. floribundus* ssp. *floribundus* forms groves consisting of about 50 trees on canyon sides in its native habitat. That the fossil tree locality represents the remains of an extensive grove can be assumed from the evidence that all the trees



FIGS. 3-6. *Lyonothamnoxydon nevadensis*: 3, transverse section showing slightly angular pores, semi-ring porous distribution; 4, transverse section showing rounded pores and diffuse porous distribution; 5, radial section; 6, tangential section; 4-6, from holotype. All are $\times 160$.



FIGS. 7-10. *Lyonothamnus floribundus* ssp. *asplenifolius*: 7, transverse section showing ring porous distribution of pores; 8, transverse section showing diffuse porous distribution; 9, radial section; tangential section. All $\times 160$; 8, 9, and 10 from one specimen, 7 from another.

lie at the same horizon in the sediments, they were preserved where they grew, and only one kind of tree is represented.

The fossil record shows that *Lyonothamnus* had a wide distribution throughout western United States during the middle and late Tertiary (Axelrod, 1940a; Wolfe, in press), and was particularly in evidence during the late Miocene in western Nevada only 50 miles north of Fish Lake Valley. Its maximum extension so far recorded was during the Miocene when it ranged from west-central Washington south to southern California and eastward into western Nevada. For reasons not entirely understood, its range became greatly restricted since the mid-Pliocene. Increased aridity and colder winters undoubtedly contributed to its disappearance in the eastern part of its range, and the increasing depression of winter temperatures towards the end of the epoch probably affected its northern distribution. At the present time it occurs naturally only on the channel islands off the coast of southern California.

Morphological variations in the leaves of *Lyonothamnus* in different parts of its range through space and time suggest that there were genetic variants in the genus at least until late Pliocene; even now there are two subspecies (Raven, 1963). Axelrod (1958) has shown that leaves of the mid-Miocene *L. mohavensis* Axelrod were half the size of the modern *L. florioundus* ssp. *asplenifolius* and the upper Pliocene form from coastal central California was intermediate. Wolfe (in press) describes a distinctly different form from the late Miocene Stewart Spring flora from west-central Nevada which he calls *L. parvifolius*. These leaves characteristically have 7-9 leaflets as opposed to five in the modern species. There is also a difference in lobation. Wolfe suggests that the northern segregates of the genus became extinct, while the southern form (or forms) gave rise to the modern species.

Whether the trees in Fish Lake Valley belonged to the northern or southern segregates one cannot say on the basis of the information available from the wood. Inasmuch as we are dealing with only one species whose associates remain unknown, we can only speculate as to where its affinities lie.

The proximity of the Stewart Spring locality to that of the fossil trees may suggest a close relationship floristically despite the slight difference in age. The Stewart Spring flora, according to Wolfe, is mesic in aspect and, although distinct from contemporary floras to the north and south, is more closely allied to the northern floras. The early Pliocene Esmeralda flora (Axelrod, 1940b) from the east flank of the Silver Peak Range a short distance east of Fish Lake Valley is arid in aspect and appears to have affinities to the south. All but two of the thirteen species described occur also in the mid-Miocene Tehachapi flora 200 miles to the south, whereas only five occur in the Stewart Springs flora. The Esmeralda flora is very small and may not give an adequate picture of the vegetation of the time. It is interesting to note that growth rings in the fossil wood fragments are narrow and average less than a mm in width, suggesting

the possibility that the climate was somewhat dry during the lifetime of the trees.

It is highly probable that the trees in Fish Lake Valley are not con-specific with the extant species of *Lyonothamnus*. It is quite possible, also, that more than one species existed in the southern Great Basin during late Miocene time and possibly into early Pliocene time.

It is tempting to try to reconstruct the sequence of events that led to the preservation of this ancient grove of trees. In western Nevada 11 million or so years ago the Sierra Nevada did not present the great barrier to circulation of moisture-laden air from the ocean that it does now. Narrow growth rings point to a fairly dry climate, but contemporary faunal beds show that the surrounding vegetation supported a wide variety of animals such as camels, horses, dogs, cats, bats, beavers, rhinoceros, etc. (Stirton, 1939). That there was some topographic relief in the area where the trees grew is indicated by the depth of the alluvial sediments in which they are buried.

The trees all appear to have fallen in the same direction as if felled at the same time and by the same agent, such as a flash flood or a wind or both. The position of the trees indicates that the destructive force came from the northwest. They were not deeply buried at first, for the absence of crown, bark, and secondary cell walls shows that a certain amount of destruction by microorganisms or other agents had occurred prior to final and complete burial to a depth at which aerobic saprophytes could not function. Further degradation was halted; the tissues subsequently became infiltrated with silica-bearing water; and the process of preservation was begun. Later the whole area was uplifted. The soft sediments offered little resistance to the erosion which resulted in the interesting sculptured effects that can be observed there today and in the exposure of the now thoroughly silicified stumps and fragmented logs.

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DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

Beginning with this issue, *Documented Chromosome Numbers of Plants* will appear in a new format. The reasons for this are several: 1. preparation of the manuscript for the printer is easier and there is less chance for error; 2. a paragraph rather than a tabular arrangement is less expensive to set in type; and 3. additional kinds of information can be included more readily. At times it may be desirable to include a sentence or two explaining the significance of a particular count, to comment on it briefly, to include a photomicrograph or a figure, or to make a new combination. It is to be understood that the collector and the counter are the same unless otherwise noted. For further instructions see Madroño 9:257-259. 1948.

Aquilegia nevadensis Boiss. $2n = 14$. Spain, Sierra Nevada, Puerto de la Ragua. Merxmüller & Grau in 1962, M. Counted by Grau.

Artemisia nana Gaud. $2n = 18$. Switzerland, Wallis, Saas. Zollitsch in 1961, M. Counted by Damboldt.

Bouteloua brevisetata Vasey. $n = 20$. Texas, Presidio Co. F. W. Gould 9718, TAES.

B. rothrockii Vasey. $n = 20$. Arizona, Pinal Co. F. W. Gould 10028, TAES.

Bromus macrostachya Desf. $n = 28$. Texas, Brazos Co. F. W. Gould 9513, TAES.

Carduus argyroa Kze. $2n = 26$. Italy, Sicily, Syracuse. Podlech in 1961, M.

C. velebiticus Borb. $2n = 16$. Yugoslavia, Dalmatia, Zadar. Podlech in 1960, M.

Carex acutiformis Ehr. $2n = 78$. Germany, Bavaria, München. Hertel in 1963, M. Counted by Dietrich.

C. alba Scop. $2n = 54$. Germany, Bavaria, Pupplinger Au. Klofat in 1963, M. Counted by Dietrich.

C. argyroglochis Horn. $2n = 68$. Germany, Bavaria, Garmish. Oberwinkler in 1963, M. Counted by Dietrich.

C. atrofusca Schkur. $2n = 40$. Switzerland, Silvretta, oberes Fimbetal. Dietrich in 1963, M.

C. austroalpina Bech. $2n = 38$. Italy, Riveria, Alassio. Podlech in 1960, M. Counted by Dietrich.

C. brizoides Jusl. $2n = 58$. Germany, Bavaria, Reichenhall. Oberwinkler in 1963, M. Counted by Dietrich.

C. camposii Boiss. & Reut. $2n = 68$. Portugal, Sierra de Maraon. Poelt in 1962, M. Counted by Dietrich.

C. cuprea (Kük.) Nelm. $2n = 70$. Nyasaland, Lake Kauline, Nyaka Plateau. Robinson in 1959, M. Counted by Dietrich.

C. curvata Knaf. $2n = 58$. Germany, Bavaria, Regensburg. Dietrich in 1963, M.

C. duriei Steud. $2n = 52$. Spain, Prov. Oviedo, El Pedregal. Merxmüller in 1962, M. Counted by Dietrich.

C. ericetorum Poll. var. *approximata* (All.) K. Richt. $2n = 30$. Switzerland, Graubünden, Ardez. Dietrich in 1963, M.

C. flavella Krecz. $2n = 60$. Italy, Dolomites, Prodoiojoch. Podlech in 1961, M. Counted by Dietrich.